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THE UNITY OF THE GNATHOSTOME TYPE

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SINCE zoölogists have recognized the simple nature of the Cyclostome fishes there have been many contributions to our knowledge of their structure and many discussions as to their nature and their true zoölogical position.

The increase in our knowledge of the anatomy of amphioxus and the clearing up of its development by the investigations of Kowalevsky, Hatschek, and Willey, have increased the amount of interest in these discussions and have added to the subject an entirely new phase in that the amphioxus, instead of being longer considered a zoölogical curiosity, a degenerated or aberrant form, has become the center of an intense and searching discussion of the origin and relationships of the Vertebrata; and amphioxus has thus come into its own by being recognized as an ancestral form in the genealogy of the vertebrate stock and the oldest living relative and representative of this group of animals.

We can now see clearly enough that the Marsipobranchia and the Acrania both stand in the relation of ancestors to the vertebrates above them, and there is no longer any doubt, while recognizing to the full the many unsolved problems in connection with its structure and development, that amphioxus belongs to the group of forms, the Prospondylia, predecessors of the Archicrania, from which the Cyclostomes are directly descended. It must be admitted that the gap between amphioxus and Bdellostoma is very great, both as regards time and the amount of the transformation of structure which it has undergone, and that in many things we cannot yet satisfactorily explain the manner in which this transformation has come about.

On the other hand, we may with certainty say nearly as much about the gap between the Cyclostomes and the other Gnathostomes, but the absence of complete knowledge has never been permitted to blind unprejudiced minds to the just estimate of the known facts in any zoölogical problem.

Recent advances in our knowledge of the Marsipobranchs render Haeckel's estimate of the amount of difference between the Cyclostomes and vertebrates above them quite untenable.

He says (*Syst. Phylog.*, vol. 3): "Eine tiefe morphologische Kluft und ein entsprechend langer historischer Zwischenraum trennt beide Classen der Agnathonen nicht bloss von den echten Fischen, sondern auch von allen übrigen Vertebraten die wir in der Hauptgruppe der Amphirhinen oder Gnathostomen zusammenfassen."

There is no reason why we should, at the present time, follow partisans of any genealogical theory of the origin of the vertebrates in ignoring the many anatomical and embryological facts which we now possess and which clearly enough establish the genetic relations of these forms.

Some writers are too prone to assume the existence of large groups of extinct forms intermediate between the groups of existing vertebrates and between these and those forms from which the vertebrates have descended — which have disappeared without leaving any trace of their structure in recent forms.

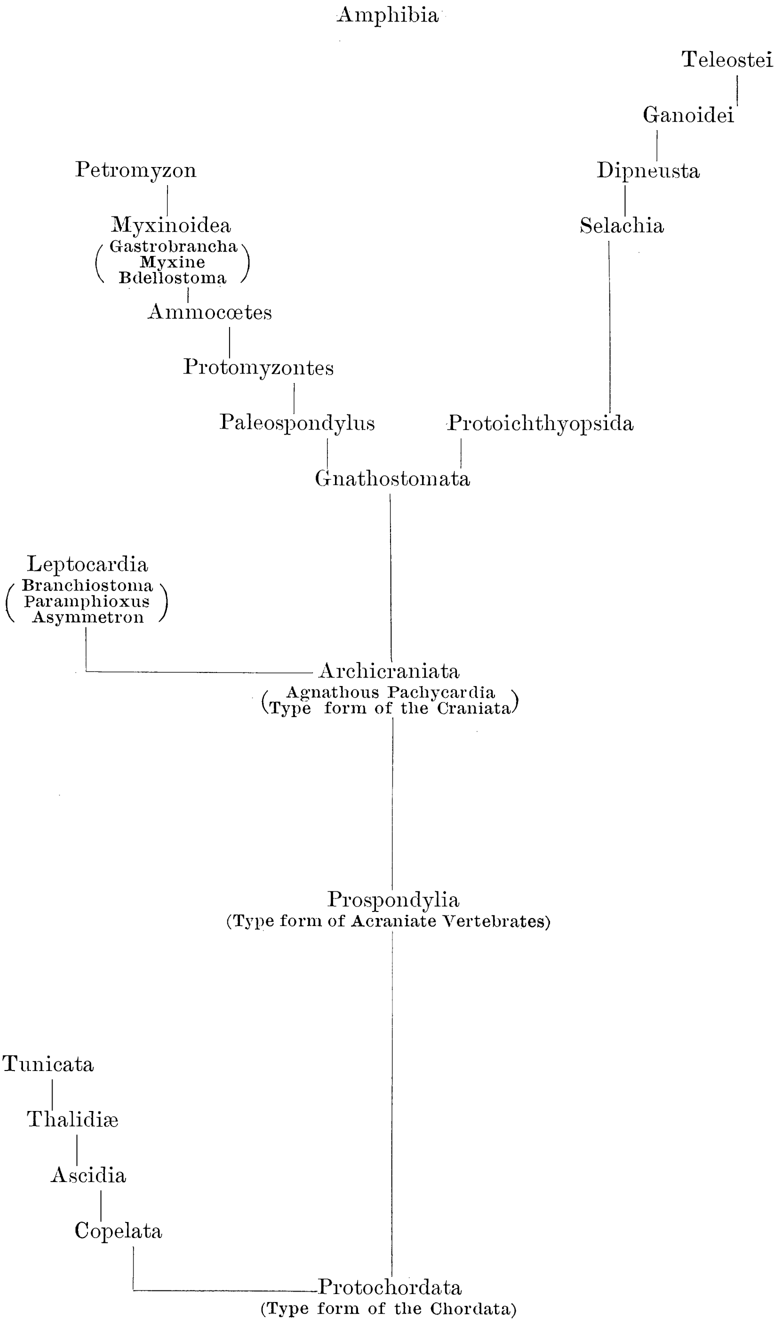
There is neither anatomical nor embryological ground for the removal of amphioxus from the vertebrate class, and we may express our view of the relation of existing forms thus:—

VERTEBRATA

Amphioxus — Leptocardia — Acrania
All others — Pachycardia — Craniata

and by the following table:—

GENEALOGICAL TREE OF THE ICHTHYOPSIDA



Before taking up the question of the unity of the Gnathostome type, a brief consideration of some of the general features of the vertebrates will clear the way for a better understanding of the arguments and facts which bear on the solution of the problem.

First of all we may well consider amphioxus as a typical ancestral vertebrate.

The Vertebrata, as we find them to-day, form a morphological unit in much the same way that the birds form a closed group — and it is only through paleontology that the shading off of the group into lower forms is to be found or proven. That the vertebrates have arisen from a common source is a statement which cannot to-day be questioned, for the present state of our knowledge of their anatomy, ontogeny, and physiology is a practical demonstration of the problem. Each increase in our knowledge only makes the demonstration stronger. All three fields of investigation — comparative anatomy, comparative embryology, and paleontology — unite in one affirmation of this fact. All three show that there has been an orderly progression (to use only living forms as examples) from amphioxus to man. No one can read Hasse's *Das natürliche System der Elasmobranchier,* to mention only one of many similar investigations, without having the fact of the historical succession of these early vertebrates indelibly impressed upon his mind. The genetic relationships of this procession of Selachians from the earliest geologic ages, when the fossiliferous records of the vertebrate stock were begun, is proven by the comparative morphologic study of the skeletons of extinct and recent forms and this proof is strengthened by the as yet only partial, embryonic record which has been worked out by many investigators. The course of development is marked by the retention in all living forms of all the divergent branches of vertebrates, from amphioxus up to the mammals, of the same fundamental arrangement of organs and systems of organs, and by the same general cellular structure. The variations in arrangements of the organs and the differences in the histological details of the tissues are not greater than the variations of the external form or of the shape of the internal organs. These are large facts of fundamental value, and have a greater morphologic worth than the many minor variations can possibly have, even when taken together. They prove the essential unity and genetic relationship of all the Vertebrata.

Semper's view that amphioxus is not a true vertebrate has long since been effectively disproved, and the most forceful part of the proof that amphioxus does belong to the ancestral stock of vertebrates is contained in its simple palingenetic development, at least so far as the earlier stages are concerned.

The method of laying down the gills up to the time that the secondary gills are established, is in every way comparable with the processes of gill formation in Bdellostoma. The transformation of the brain up to the apex of its development is similar to the development of the vertebrate brain, the only difference being that it stops its growth in a very primitive stage of the Craniate brain. The differentiation of the tissues is in every respect the same as that occurring in other vertebrates, except that the process of tissue formation does not go as far, while some tissue systems, which appear in upper vertebrates, are never developed in amphioxus. For example, the masses of connective tissues common to other vertebrates, in the form of true cartilage and bone, are not even hinted at. The statement that its tissues are epithelial is most erroneous.

The lack of formation of such structures as jaws, chambered heart, lacunar hepatic gland, cartilaginous skull, etc., is certainly to be put down as a palingenetic characteristic.

When we seek the type form of the vertebrate stock we are forced to look to the invertebrates as the source of origin. Almost all the groups of the Metazoa have been searched for the ancestral type, and in nearly every case a type-form has been discovered which shows the means of descent sufficiently satisfactory to the individual zoölogist to warrant a long and careful discussion of the manner in which the morphologic and physiologic changes have come about that have resulted in producing the vertebrates as we find them to-day.

Three types of structure have, however, been used more frequently than the others. They are, respectively, nemertean, annelid, and arthropod. All three of these types possess a sufficient number of characteristics in common with the vertebrate type to warrant many parallels being drawn between each of them and the vertebrates.

The great difficulty in the way of accepting any of the well developed jointed invertebrates as the ancestral vertebrate type lies in the necessity of a revolution of the body through an angle of 180 degrees, whereby the dorsal surface of the invertebrate becomes the ventral surface of the vertebrate; and also in the concomitant necessity of the formation of a new mouth and the total disappearance of any trace of the old mouth. While there is, at the present time, abundant evidence to show that the functional mouth of the vertebrate of to-day is a neomorph, and that the original mouth was situated at a point anterior and dorsal to the present location, it does not follow and the evidence does not tend to show, that the old mouth corresponds in any way to the mouth, *e. g.*, of the arthropod.

This translocation of the mouth from the invertebrate ventral to the vertebrate ventral surface must have been connected with the reduction of the circumœsophageal nerve ring, and with the total disappearance of that section of the stomodæum which connects the mesenteron with the mouth by preforating the nervous system through the territory of the circumœsophageal nerve ring.

The fact that the stomodæum no longer perforates the nerve ring is a fact which must be satisfactorily explained by in some way discovering the stages through which the transformation has passed from the invertebrate to the vertebrate condition, or the genealogy of the vertebrate stock with the arthropod as the ancestral form cannot be satisfactorily explained.

There is great doubt that the vertebrates are derived from a highly organized annulate invertebrate. They are more probably a distinct branch split off from the unsegmented worms, and developed independently. Many are the theories which have been offered to harmonize the annulate and the arthropod conditions with the vertebrate, but none of them have accounted for a sufficient number of facts to warrant their general acceptance, and, as above stated, the main difficulty has consisted in the inability to picture the revolution of the invertebrate body in such a way as to make it physiologically possible in living forms.

It matters not what position we take with reference to the origin of the vertebrate stock, when we arrive at the stage of development represented by amphioxus we are compelled to admit, in the light of our recent knowledge, that amphioxus is a true vertebrate, lacking it may be the first trace of the craniate skeleton, and lacking many of the other features which are characteristic of most of the existing vertebrates, but is nevertheless, the only existing form which serves as a connecting link between the simple ancestral type of structure and the more complex anatomical and physiological conditions of the higher vertebrate.

Some zoölogists have recently re-uttered Semper's opinion, that amphioxus is not a true vertebrate, but such restatement of Semper's opinion is justly to be compared to the restatement of the opinions of the older zoölogists, who at various times held amphioxus to be a worm, a mollusc, and a tunicate. Instead of making assertions as to what amphioxus is or is not, the only scientific method of solving the problem of its actual position in the animal series is by a careful study of its structure and a comparison of this with the structure of the lower vertebrates. Such comparison proves beyond the shadow of a doubt the relation of the amphioxus to the lowest fishes.

A review of some of the salient features of amphioxus' anatomy will not be out of place at this point. As regards the form of the body, all zoölogists recognize the fact that the shape of the vertebrate body is a result of the direct response of the organism to its environment, particularly the necessity of locomotion. The lancet shape of amphioxus is due to its burrowing habit. The lack of paired appendages is due to the fact that amphioxus represents the stage of the development of vertebrate structure when such appendages had not yet been developed. The median fin folds are well developed, both in the head and in the caudal region, and serve the same function in essentially the same way that they do in other vertebrates. There is no trace of a *quasi* lateral fin fold, nor of the buds of lateral appendages in the amphioxus, but neither of these are found in the Cyclostome fishes, which are much more highly organized than amphioxus.

The lack of the development of paired appendages in amphioxus and the Cyclostomes is not a mark of degradation, or degeneration, as some zoölogists would put it, because the whole course of their development and the facts of their morphology prove conclusively that these structures were not called forth by the response of these animals to the stimuli of their environment in the direction of pedal locomotion on the sea bottom. It is highly probable that these appendages arose as ventrally projecting bar-like structures, to enable the bottom-living forms (since all were bottom dwellers to begin with) to move more readily from place to place on the surface of the sea floor while remaining in contact with the sea floor, thus avoiding the necessity of the more difficult feat of balancing themselves in the lighter ambient fluid above the earth floor, in the effort to effect a change of place.

Paired appendages then *did not arise as fins* for the purpose of *balancing the animal in the water*, but the paired fins of fishes have been developed by the transformation of the primitive paired organs of locomotion, of which the paired appendages of the Amphibia and their descendants are the direct and, in their simplest forms, the least modified derivatives.

When one studies the life habits of amphioxus and Bdellostoma in their natural element and, at the same time, the history of their development, he no longer entertains the idea that these animals have lost paired appendages once possessed by their ancestors, but will, and can only, say that they are the ancestral forms of animals possessing paired appendages, and that in the case of amphioxus and of Bdellostoma we have two stages in the response of the vertebrate stock to the stimulation of the environment looking toward the formation of locomotor appendages.

They are both bottom dwellers of necessity, although they take occasional excursions into the superambient water, but quickly fall back, from the force of gravity, to the bottom. These excursions into the superambient liquid are effected by the motion of the caudal fin from side to side. This fin is the main organ of locomotion used by all fish-like vertebrates for progression through the water.

When amphioxus strikes the bottom after such an excursion, it lies quietly upon its side, since it is unable to coil its body sufficiently to lie on its ventral edge. Most of its life it passes buried in the sand. To enter the sandy bottom in which it lives, it first makes an excursion into the superambient water and then descends head first upon the sandy bottom, boring its way among the particles of sand. When swimming it maintains its body in the dorso-ventral position.

In the case of the Bdellostoma we have a very different condition. The Bdellostoma possesses a body remarkable for its flexibility and its elasticity, and is fitted not only to swim in a dorso-ventral position, but during life, when it rests upon the bottom, always does so with a dorso-ventral orientation. While amphioxus shows a distinct inability to orient itself and maintain equilibrium in this position for any but the shortest periods of time, Bdellostoma exhibits in a high degree the capacity to maintain its position with ease, accuracy, and for an indefinite period. This capacity for the equilibration of its body without the possession of paired appendages is both remarkable and deserving of more careful study than has yet been given.

With the possession of a simple ear, the tubular portion of which lies in one plane of space, and with the lack of equilibrating paddles in the form of pectoral and pelvic appendages, Bdellostoma maintains its position while in motion with at least as great precision and as great apparent ease as any of the vertebrates possessing paired appendages.

It is clear, then, that it is not the necessity for the equilibration of the body that has brought about the development of the paired appendages in the vertebrate stock.

Since the formation of the paired appendages in all other water dwellers besides fishes is for the purpose of moving the body over the bottom, that is locomotion, it becomes very probable that the fish fin is a secondary structure, derived from the primitive pedal appendages, which were used by the ancestral form exclusively for locomotion.

This effectively disproves the theory of Gegenbaur of an ancestral archipterygium, and the Thatcher-Balfour lateral finfold theory, and it removes from the field of vertebrate morphology one of the most difficult problems which it has been called upon to solve, by simplifying the conditions of the problem.

While Bdellostoma is able to swim with ease, accuracy, and precision, and thus change its position in space either for the purpose of capturing prey, avoiding its enemies, or seeking a new position upon the bottom, it is not able to progress upon the bottom except by using the same swimming motion of its caudal region which enables it to progress through the water. It cannot be said, however, to possess the power of locomotion except by swimming or springing. Undoubtedly the next step in the transformation of the Bdellostoma-like body of the ancestral Gnathostome was the gradual formation of pedal appendages, which enabled it to move easily, certainly, and symmetrically over the bottom.

It is just as erroneous to maintain any hypothesis which would derive the paired appendages of the Amphibia, for example, from the paired fins of fishes as it is to maintain the claim that the pectoral appendages (arms — forelegs) of land vertebrates are derived from the wings of birds.

When we consider the structure of the nervous system we are again brought face to face with the fact that amphioxus represents a developmental stage in the central nervous system repeated by other members of the vertebrate stock. Its nerve cord possesses all the relations to the other main organs of the body that are possessed by the central nervous system of other vertebrates. It lies immediately above the dorsal surface of the notochord in the hollow skeletal tube composed of a connective tissue membrane, in the walls of which, however, no chondroidal tissue is formed, and in which no calcareous matter has at any time been deposited, but this condition of the protective tube of the central nervous system is reproduced in the development of all the other vertebrates, from the amphioxus to man. This tube is not surrounded by skeletal structure in the amphioxus, but it is perforated with lateral openings made through its lateral face for the exit of the nerves passing out from it and entering it. In this it is also in harmony with the conditions found in all other vertebrates.

In the antero-posterior direction, the nerve tube is divided into two main parts, as in all other vertebrates, a brain and a spinal cord. While there are differences of histological value between the spinal cord of amphioxus and higher forms, this difference is hardly greater than exists between species of the higher vertebrates above it.

We may dismiss further consideration of this part of the nervous system with the statement that it is in every respect a vertebrate spinal cord. When we come to consider the structure of the brain, however, we find a simplicity in the arrangement of the parts, which has until recently been an obstacle to most zoölogists in establishing the homologies between the amphioxus brain and the brain of the Craniata, and even to-day very few anatomists know enough about the structure of amphioxus to be able to establish the homologies which are existent.

Apparently the first zoölogists to note the presence of the amphioxus brain were Leuckart and Pagenstecker, who homologized the entire brain vesicle of amphioxus with four ventricles of the Craniata.

Owsjannikow later held the same view. In 1858, Professor Huxley, after careful examination, decided that the amphioxus neurocœle was the equivalent of the thalamencephalon of the Craniata.

In 1860, Wilhelm Müller concluded that it corresponded with the thalamencephalon and the prosencephalon of the Craniata. He further determined the location of the pigment in the anterior end of the brain tube and found that the pigment granules were located in the anterior ends of the brain cells. He also discovered that the olfactory pit was connected with the anterior end of the brain.

In 1861, Langerhans discovered the true relation of the olfactory epithelium of the olfactory tubercle of the brain. He decided that the amphioxus brain included the whole of the primitive Craniate brain.

In 1891, I described in a brief way some of the anatomical features of the amphioxus, giving the following account of the brain. "The anterior end of the neural axis of amphioxus is a brain and corresponds with a certain definite portion of the brains of other vertebrates. Its anterior wall is the homologue of the lamina terminalis of other vertebrate brains, and the anterior portion of its unpaired ventricle is the thalamocœle."

"I would define the vertebrate brain as follows: the 'vertebrate brain' is that portion of the anterior part of the axial nerve cord, associated with organs of special sense, containing an enlargement of the central canal, which is carried out into all structures formed by the outgrowth of the brain wall. Its walls contain the principal centers for the coördination of sensations and movements. All further additions to this simple brain (amphioxus) are made in response to the demands of the organs of special sense, with which is associated extension of the coördination apparatus. With such additions we have the compound brain of all other known vertebrates up to man, inclusive."

"Reasons why the anterior end of the nerve cord of Amphioxus is a brain. It is a brain because: —

1. It forms the anterior termination of the neural axis.
2. It stands in intimate relation to the sense organs, eye, and nose.
3. It gives off at least two pairs of sensory nerves provided with peripheral ganglia.
4. It possesses large groups of ganglion cells forming centers of coördination.
5. It possesses an enlarged section of the central canal in the form of an unpaired ventricle with three well marked diverticula — two optic, one olfactory.
6. It is the largest part of the nervous system, at a time when the massive musculature and branchial apparatus of the anterior middle fourth of the body have not reached the stage requiring much enlarged central accommodations.
7. It shows in young larvæ growth to such an extent as to cause a ventral flexure of the chorda, while the brain itself bends downwards and so produces a "cranial flexure."
8. It shows in all other details of structure that *it is not* simply the *anterior end of the spinal cord,* but a *brain.*
9. It shows in a larval stage, soon after the differentiation of fibers in the neural axis (larvæ with one gill slit), a marked differentiation into ganglionic and fibrous regions, and the boundaries of the unpaired ventricle as well as of the lamina terminalis are distinctly marked out. There is then a ventricular segment of the brain reserved for the special sense organs. The fibers appear simultaneously with the formation of the pigment spot, and are in all probability the ways by means of which the sensations from this special sense organ are conveyed backward to the motor centers.
10. Since amphioxus is a vertebrate, these relations *must* have direct and important bearings on the phylogeny of the vertebrate brain and head, and will afford us invaluable aid in clearing up these intricate problems."

"The large collections of ganglion cells just posterior to the thalamocœle are homologous with the medullary nuclei of other vertebrates, since their connections show them to be centers for the control of the branchial apparatus, and the sensory and motor structures lying in the territory of the gill basket, *e. g.*, centers of respiration, deglutition, etc."

"The ontogenetic changes of the neural axis in other vertebrates carry the brain through the condition which in amphioxus remains permanent as the adult brain."

As regards the eye, I announced in 1891 that the eye-spot of amphioxus — that is to say, the unpaired but bilaterally symmetrical patch of epithelial cells lying in the lamina terminalis of the amphioxus brain — is the forerunner of the vertebrate eye, and that, as regards its physiology, it was not a visual organ nor an organ of sight, but an organ for the perception of the variations in the intensity of light.

This pigmented patch of epithelium occupies the same position in the adult amphioxus that the unpaired but bilaterally symmetrical patch of pigmented cells in the embryo sturgeon, as described by Kupffer, and in the embryo of Galeus, as observed by me, does with reference to the lamina terminalis of the brain of these forms.

In both the latter cases the pigmented patch is converted into the recessus opticus, and the recessus opticus gives rise by a process of evagination to the two optic vesicles.

Amphioxus, therefore, presents us with an adult condition which is represented in the higher vertebrate form by the simple condition of the brain wall in the earlier stages of the development of the nervous system.

For a fuller discussion of the anatomical conditions present in the adult amphioxus see my paper (*loc. cit.*, pages 238 to 234).

It is clear from this description of the lamina terminalis in the embryos of the sturgeon and of the dog-fish that the early stage of the eye in fishes is truly comparable, indeed is homologous, with the eye organ in amphioxus and is developed in identically the same way. As I have already pointed out, the pigment in the eye of the amphioxus lies in the inner end of the cells forming the anterior end of the neural tube.

In the sturgeon this pigmented area on the inner face of the anterior brain wall is subject to the evagination process, being carried out with the cells of the recessus opticus.

My conclusions with reference to the eye of amphioxus were based upon a very extensive study of the eye of both the old and the young of amphioxus, and I was able to show that there is a great diversity in the form of the pigment area in different members of a series of individuals and that there is a tendency for the pigment area to divide symmetrically on either side of the median line.

Of greatest moment, therefore, are my observations and those of Kupffer which show that the pigment to be later used in the retina of the eye is first of all laid down in the inner ends of the cells of a primitively unpaired, even though bilaterally symmetrical, plate of cells which evaginates from the brain as the recessus opticus.

Minot attempts to homologize the vertebrate eye and optic tract with the highly differentiated arthropod eye, supra-esophageal ganglion and the circumesophageal nerve ring, but the idea that the visual organ of the vertebrates is to be sought for in such a specialized organ as the compound eye of arthropods is unsupported by morphological facts.

The nose in amphioxus remains in the form of a conical epithelial pit, whose apex is connected with or is in contact with the anterior end of the brain.

This pit is the so called sinus olfactorius impar, being the remains of the anterior neuropore. The right and left walls of this conical pit are thus morphologically equal, and, notwithstanding the fact that the pit is later pushed to one side by the growth of the base of the median fin-fold, we must hold that it is bilaterally symmetrical both in origin and in adult life and is strictly comparable to the plate of cells which evaginates from the anterior end of the brain of Bdellostoma and of the sturgeon, and which has been conveniently called the unpaired nasal plate.

It has long been accepted that the nasal epithelium of the Gnathostome vertebrate is laid down as a pair of bilaterally symmetrical plates in the embryo and continues paired throughout life, while in the Cyclostome it is laid down in an unpaired condition and ever remains so. Nothing could be more incorrect, for the plate in some Amphibia is identical with that in the Cyclostomes. It is a single patch of cells symmetrically placed with reference to the sagittal plane of the body. In reality it is a double patch, although the indifferent tissue, which later forms a septum, has not at this stage developed.

It is said that in Acipenser embryos a median unpaired nasal plate precedes the paired nasal organ. This being the case, we have all the more reason to consider the Marsipobranch nose a paired structure, even though it appears to develop from an unpaired plate.

There is certainly no truth in Haeckel's dictum that "the pharyngo-nasal canal [of Myxinoids] is a secondary acquirement in connection with parasitic habit."

Notwithstanding that much has been said about the naso-pharyngeal tube of the Myxinoids, the full significance of this structure has not yet been made out. While it at first seemed to be an organ at the height of its development in Bdellostoma, the embryological evidence would indicate that it is a very old structure. We should not forget that in the Petromyzontes it is already closed off from the pharynx, and that in all other vertebrates it arises in a very early stage of embryonic life as a naso-hypophysial invagination of the ectoderm towards the mesenteron. It would thus seem to be on the verge of extinction in the Cyclostomes. No other stages of its development are known to us.

The total absence of an auditory organ in amphioxus is held by certain zoölogists to be a difficulty in the way of accepting this animal as an ancestor of the vertebrate stock.

They point out that in the tunicates, especially in the Appendicularia, there is an otocyst with inclosed otolith, which supposedly serves as an organ for the perception of wave motion in the water. It is also held that, since the tunicates stand in genetic relationship to the vertebrate stock, it is very unlikely that any form intermediate between them and the vertebrates would entirely lack an auditory organ. The error in their reasoning lies in the fact that they assume that the auditory organs of the tunicates and the vertebrates are homologous structures.

This is not the case, as all the evidence, both morphologic and ontogenetic, clearly proves. The vertebrate auditory organ is a neomorph arising within the vertebrate stock, from a sense-organ rudiment entirely absent, so far as we yet know, from the tunicates. So that the absence of an ear from amphioxus is fully accounted for, at least in so far as relation to the tunicates is concerned. The tunicate ear is, in a strict sense, an otocyst, and not an ear.

With reference to the segmentation of the body of amphioxus, all the evidence seems to point to the ancestral character of this segmentation in relation to mesodermic segmentation of the higher vertebrate forms, with the exception of one peculiarity, which is probably palingenetic in its nature, but which, so far as we know, does not occur unmodified in any other vertebrate. I refer to the origin of the mesodermic segments from two bilaterally placed hollow pouches pushed out from the mesenteron.

From the many indications which have been discovered by numerous investigators, the mesoderm in the higher forms follows this plan of origin, but the architecture of the transformation is cœnogenetically very much shortened and changed, as in the case of many other organs of the body.

There is no occasion to dismiss all the pertinent indications preserved in the higher forms which indicate that this method of origin was the primitive one, simply because complete and well formed diverticula are absent from the ontogeny of the mesoderm in all vertebrates above amphioxus that have yet been investigated.

Regarding the suggested affinity between amphioxus and the annelids in this matter of the segmentation of the mesoderm, the unprejudiced mind will not hesitate to make the conclusion that it is far less intimate than the relationship already described.

The difficulties surrounding the establishment of the homology of the reproductive organs of amphioxus with those of the higher vertebrates are certainly not solved by any reference of the vertebrate stock to the annelids as ancestors, for the difficulty complained of by Minot that the reproductive organs appear segmentally in amphioxus, but non-segmentally in other vertebrates, is only increased by carrying the ancestral vertebrates back to the annelids, for here the segmental arrangement of the gonads is even more primitive and is accompanied by many annelidan characters of the other organs of the body, which carry us farther than ever away from an explanation of the origin of the internal sexual organs of the vertebrate body. Certainly, when we have to choose between annelids and amphioxus for an ancestor of the vertebrates, it would be giving up much we have already gained to go back to the vermian type when we have an animal such as amphioxus, possessing many of the vertebrate characters already developed and showing a stage of organization which no one can for a moment doubt is immediately below that of the vertebrates and far removed from that of the annelids and tunicates. It is good occasionally for the zoölogist to view in the large and in perspective the whole animal and to take note of the interrelationship of all its parts, together; in other words, to take a "bird's-eye view" of the form being studied in order that minute and occasional differences, which our incomplete knowledge does not yet permit us to explain, shall not be unduly magnified and thereby be given an importance entirely unwarranted, and thus prevent our establishing the homologies and recognizing the real genetic relationships of the form in question. Much that has been said about amphioxus in recent years has been in the nature of zoölogical quibbling, a playing with non-essentials and an ignoring of the fundamental facts of the anatomy and development of this creature.

The intestinal tract of amphioxus also represents an ancestral condition, which is passed through ontogenetically by higher vertebrates. The liver pouch always arises as an unpaired diverticulum of the mesenteron, which later becomes established as a pair of diverticula higher up in the phylum.

As regards the other features of the intestinal tract, they remain in a very primitive condition, and in the Cyclostome we have a decided advance towards the condition occurring in higher forms. In the Cyclostome the liver becomes a massive gland, with the characteristic vertebrate structure, but neither amphioxus nor the Cyclostomes possess a pancreas.

The mouth in amphioxus is extremely primitive and shows no traces of skeletal structures which may yet be safely homologized with the maxillary and mandibular appendages of the Cyclostomes and the vertebrates above them.

The endostyle, which exists in a high state of development in amphioxus and which is well preserved in the larval Ammocœtes, possesses as its function the collection and transference of food to the pharynx. During the transformation of larval Ammocœtes into the adult Petromyzon the organ is functionless. Beginning with the adult Cyclostome, and from there on throughout the rest of the vertebrate series, its remnant forms the thymus gland.

As regards the excretory organs of amphioxus, the researches of Boveri show that they are segmental in nature and that each tubule opens upon the surface of the body, no collecting duct being formed. Even on the theory of the annelidan origin of the vertebrates this is a stage of development through which the vertebrate ancestors must have passed, and instead of being an argument against the close genetic relationship of amphioxus to the vertebrates above it, it is one of the best examples we have in all zoölogy of the persistence of an extremely primitive condition of an organ, even after the general advancement of the body, in a morphological sense, makes the presence of such segmental organs appear out of place and not in harmony with the stage of development of the organism as a whole.

A similar instance of the persistence of primitive excretory organs in the adult condition is furnished by Bdellostoma, the only vertebrate which possesses a functional pronephros in the adult condition, and when we compare the adult pronephros of the Bdellostoma with the ontogenetic condition of the pronephros as seen in mammals and in birds, we recognize at once that the differences between these two stages are greater than the differences, for example, which we find between the mesodermic segmentation of amphioxus and other vertebrates or the segmentation of the reproductive organs of the same two forms.

So that this evidence, as well as all that I have previously brought to notice, points to amphioxus as the nearest living form among the ancestors of vertebrates.

A glance at the information contained in the table given below will serve as a basis for comparing Bdellostoma with amphioxus, on the one hand, and with the higher vertebrates, on the other.

Table of some of the primitive characters (p.) of Bdellostoma which are embryonic (e.), for higher vertebrates.

1. Notochord. (p. e.)
2. And its extension to the hypophysis. (p. e.)

3. Membranous skeleton of Bdellostoma. (p. e.)
4. Simple heart. (p. e.)
5. Cranial aorta. (p. e.) (Subcordal aorta.)
6. Peritoneo-pericardial cavity. (p. e.)
7. Subintestinal vein. Ventral vein of amphioxus. (p. e.)
8. Passage of subintestinal vein through liver without capillary net (p. e.)
   Persistent subintestinal vein, which passes around portal system.
9. Gill arteries correspond to gill arches, not to hemibranchs. (p.)
10. Vein from pronephros to right cardinal vein. (p. e.)
11. Blood from anterior body walls passes into portal system. (p. e.)
12. Contractile portal heart. (p.)
13. Origin of carotids from lateral branchial commissure. (p. e.)
14. Segmental disposition of somatic and renal artery and veins. (p. e.)
15. Frequent anastomosis between post. card. veins. (p. e.)
16. Inferior jugular veins. (p. e.)
17. Large number of gills up to 14. (p. e.)
    Functional branchial vessels; functional branchial bars or cartilages.
18. Their reduction during ontogenesis. (p. e.)
19. Functional pronephros. (p. e.)
20. Absence of genital ducts. (p. e.)
21. Brain. (p. e.)
22. Cranial and spinal nerves — separation of motor and sensory branches. (p. e.)

When we compare these characters of a Craniate with the conditions obtaining in amphioxus, we find a surprising agreement between them.

I think, from the presentation of facts just made, it is clear that amphioxus belongs to the ancestors of the present day vertebrates. It is, however, neither a Craniate nor a Gnathostome, and it is separated from all the other forms by a zoölogical gap which we cannot yet adequately measure, but which is very large. Let us now pass to a consideration of the relationships of the Craniate Vertebrata.

Let us assume, with Haeckel, that the Prospondylia are the stock from which the Leptocardia and the Archicrania both arose.

From the latter hypothetical group are developed all the Craniate forms which, down to the present time, have been classified in two main divisions: the Cyclostomata and the Gnathostomata.

In 1894, I showed that the so called tongue apparatus of the Cyclostome fishes, particularly of the Myxinoids, was developed by a transformation of the jaw apparatus from the maxillo-mandibular apparatus of some Gnathostome ancestor, and these views, together with the anatomical evidence supporting them, were printed in the *Journal of Morphology*, vol. 17, and in the *Bulletins* of the University of Cincinnati, vol. 1, nos. 1 and 2.

The development of the mouth of Bdellostoma and the pre-oral and postoral bars (the maxillary and mandibular arches) respectively in the early stages of Bdellostoma, before the formation of the tongue apparatus, adds further corroboration of the accuracy of the interpretation of the homologies of the cranio-facial apparatus of the Marsipobranchi.

With the discovery of the jaw apparatus in the Cyclostomes, the most essential character used by systematists for the separation of this group from the Gnathostomes disappears.

Many other characters, however, of which perhaps the absence of paired appendages is the most noteworthy and important, remain as a sufficient ground for a very distinct separation of these forms from the rest of the vertebrates.

But the group Gnathostomata must now include the Marsipobranchi as well as all the forms hitherto included, so that, as our classification now stands, *all* the Craniata are Gnathostomes, and, as before, the only living Acraniate is amphioxus.

The solution of the problem of the origin of the cranio-facial apparatus is thus pushed back upon the extinct vertebrate forms which fill in the gap between the common ancestor of amphioxus and Craniata. Possibly paleontology may bring us the needed information, or it may be that the embryology of some form yet unstudied will disclose the method of the transformation of the acraniate or agnathous into the craniate or gnathostome head.

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